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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

I. INTRODUCTION

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THE 1964-65 LA PLATA-HARVARD EXPEDITION

This is the first of a proposed series of papers giving the scientific results of a fossil-collecting expedition to western Argentina made during the summer of 1964-65 under the joint auspices of the Universidad de La Plata and Harvard University. The project grew out of the realization, during an earlier expedition of this sort, that further work in this area might result in important additions to the early tetrapod fauna of South America.

In 1958 a group of Harvard paleontologists under the direction of Prof. Bryan Patterson and myself, in cooperation with the Museo Argentina de Ciencias Naturales "Bernardino Rivadavia" de Buenos Aires, spent some months in exploring for vertebrate fossils in western Argentina. In part, Tertiary mammals were collected, and in part, fishes and brachyopid labyrinthodonts from the Triassic Cacheuta series of Mendoza Province (cf. Rusconi, 1951, etc., and Romer, 1960). Most especially, however, we explored and developed the Triassic beds of the Ischigualasto region in northeastern San Juan Province (cf. Romer, 1962); these proved exceedingly productive. Work on them has been continued by the Instituto Lillo of Tucumán, at first under Dr. Osvaldo Reig, currently under Sr. José F. Bonaparte.

The Harvard members of the 1958 party included, in addition to Prof. Patterson and myself, Arnold D. Lewis, chief preparator of the Museum of Comparative Zoology, James A. Jensen, then of the Harvard staff but now in charge of geological and paleontological collections at Brigham Young University (Provo, Utah), and Mrs. Ruth H. Romer. Prof. Patterson's interests have now shifted to another field. The others of the group, however,

became deeply interested in the problems of the early history of tetrapod life in South America, and felt that, if the opportunity should be presented, a second trip of exploration in western Argentina might quite possibly result in a major addition to this story.

Such an opportunity arose in 1964 through a grant from the National Science Foundation, from which could be met most of the costs of a field trip of the sort proposed. Accordingly, an agreement to this end was drawn up between the Harvard Museum of Comparative Zoology and the Museo de Universidad Nacional de La Plata. Under Argentinian law 9080 of 1911, all fossils are declared the property of the national government, under the Ministry of Education. A commission of three directors of leading museums is empowered by the Ministry to regulate the collection and disposition of fossil materials. Our agreement with the Museo de La Plata was approved by this commission. As provided by law, type specimens and other representative materials, or casts thereof, are to be deposited in the Museo de La Plata; other specimens remain the property of the Harvard Museum. Further, we are to be allowed to have for two years exclusive right to the study and description of specimens from any new fossil deposits discovered during the course of the work.

Our objective was to find fossil localities for reptiles and amphibians in horizons in the Permian or in Triassic beds earlier than that of Ischigualasto. Although the position of the Ischigualasto fauna is somewhat debatable, it is essentially middle Triassic in character, predominantly one of rhynchosaurs and cynodonts of gomphodont type; there are known a few advanced thecodonts, but only the bare beginnings of the dinosaur fauna which dominates the scene in the late Triassic. Faunas comparable to that of Ischigualasto are known in Brasil (Santa María) and in Africa (Manda beds); but while antecedent Permian and Lower Triassic faunas are abundant in Africa, almost nothing was known of earlier tetrapods in South America. On that continent no tetrapod has ever been reported from the Permian of Argentina, and elsewhere nothing is known except for the aberrant aquatic *Mesosaurus* of southern Brasil (and South Africa) and a single labyrinthodont from the Brazilian Permian (Price, 1948). The earlier Triassic was, before our recent exploration, almost equally unknown as regards reptilian faunas. It is possible that, despite general beliefs as to its late Triassic position, the Cacheuta series may be of early Triassic age (cf. Reig, 1961), but the evidence is far from conclusive, and

little reptilian material is known from this series. Recently, two forms, a dicynodont and a gomphodont, were discovered in southern Mendoza Province and are now being studied by Sr. Bonaparte; these are probably early Triassic in age.

This short list is a complete roster of all tetrapod vertebrates known from any part of South America in deposits older than the relatively late Triassic of the Ischigualasto Formation and the essentially comparable Santa María beds of Brasil. A great deal of stratigraphic work has been done in western Argentina by the geologists of the Instituto Nacional de Geología y Minería, the Yacimientos Petrolíferos Fiscales and the Comisión Nacional de Energía Atómica, and some thousands of square miles of continental deposits have been mapped as presumably Permian or Triassic in age. But apart from a few finds of fishes, not a single vertebrate fossil was discovered in any of these seemingly barren beds. It was thus not impossible that our trip might have been a complete failure, and that the entire four months planned for field work might have ended without our finding a single specimen.

Geologists, however, intent on stratigraphic work, are notoriously liable to overlook fossil materials for which the eye of the paleontologist is trained. Our obvious plan of campaign was to visit, one after another, "sample" areas in which Permian or Triassic rocks had been mapped, and to hope that, ultimately, one or more of these widespread regions might yield a worthwhile fauna. We found the geologists of the various Argentinian services mentioned exceedingly generous and helpful in giving us their advice and free access to unpublished maps, manuscripts, and field notes to aid in our laying out a plan of campaign and in discussing matters of stratigraphy and faunal succession. We wish to thank these friends for their help. They include, amongst others: Director General Félix González Bonorino, Dr. Roberto V. Tezón, Vocal del Directorio del Instituto, Dr. Juan C. Turner, Dr. Eduardo Holmberg, Dr. Francisco Fidalgo, Dr. Guillermo Furque, Dr. Emilio González Díaz, and Sr. Carlos Turcogreco, of the staff of the Instituto Nacional de Geología y Minería; Dr. Eduardo Rolleri, Dr. Miguel Flores, Dr. Alberto Mingramm, Dr. Pedro Criado Roque, Dr. Héctor F. de la Mota, of the Yacimientos Petrolíferos Fiscales; Profs. Sergio Archangelsky, Angel V. Borrello, and Alfredo Cuerda, of the Universidad de La Plata; Prof. Arturo Amos of the Universidad de Buenos Aires; Dr. Pedro N. Stipanice, director of geological work for the Comisión

Nacional de Energía Atómica; and Sr. José F. Bonaparte of the Instituto Miguel Lillo de Tucumán.

The major part of the funds which made the expedition possible was furnished by grant GB-2454 of the National Science Foundation. The cost of the motor vehicles and a fraction of the travel expense were supplied from private sources. We wish to thank Brigham Young University for allowing Mr. Jensen to accompany us, and the Museum of Comparative Zoology for making it possible for Mr. Lewis to take part. Publication of this paper was aided by NSF grant GB-4615.

Our collaboration with the Museo de La Plata proved exceedingly advantageous. Professor Rosendo Pascual aided us in every way before, during, and after our months in the field, and for a large fraction of the time was an active member of the field party. We are very grateful to Dr. and Señora Pascual for their hospitality in La Plata before and at the close of the field season. Dr. Mario Teruggi, Dean of Natural Sciences and Director of the La Plata Museum, aided greatly in solving our difficulties with the provincial government. Very welcome was the hospitality given us by the University at Samay Huasi, "the house of repose." This had been the country estate of Dr. Joaquín B. González, famous Argentinian author, statesman, and educator, and is located near the city of Chilecito in La Rioja Province. Willed by him to the University at his death, it is now used as a resort for artists, writers, and faculty members. An irrigated desert oasis of some 40 acres or so, with splendid groves of trees, vineyards, and gardens, it contains a spacious and well-equipped house, with a permanent staff. Most of our work proved to lie in La Rioja Province; Chilecito was the best available town to visit periodically for supplies, and we greatly enjoyed on these occasions the amenities afforded by Samay Huasi through Sr. and Sra. Amoretti and their staff, and Prof. Bongiorno of the University who has charge, in addition to other duties, of a museum at Samay Huasi.

Our equipment for the trip was carefully selected by Mr. Lewis, on the basis of his experience on the previous expedition, to the end of attempting to make our work under the somewhat trying conditions of summer in the arid regions of western Argentina as efficient and as comfortable as possible. For rolling stock we took with us a 4-wheel-drive Jeep and a $\frac{1}{2}$ ton stake-bodied truck, likewise with 4-wheel traction, and equipped with a 75-gallon water tank and spare gasoline tanks. Most useful, as it proved, was a "tote-gote" — a motoreyclette of a type recently

developed in the western United States for traversing rough country and steep grades, and able to carry a modest load of materials in addition to the rider. Without this, our work would have been severely handicapped, for part of our best collecting areas proved to be one or two miles from the closest point we could reach with a jeep; the laborious business of attempting to carry in on our backs many hundreds of pounds of plaster and hundreds of gallons of water, and return with some thousands of pounds of plaster blocks, would have greatly reduced our results.

Our party arrived in Argentina the latter part of October, and set out for the field after a short stay in La Plata and Buenos Aires to complete our equipment and obtain all possible data and advice. We then began our planned series of visits to typical areas of sediments mapped as presumed Permian or Triassic in western Argentina. As the discussion above would suggest, our expectations of success at any given locality were none too sanguine, and for the first two months of the trip our gloomiest forebodings appeared to be realized; during this time we failed to find the slightest scrap of tetrapod bone in any new area.

The Santa Clara Formation occupies a considerable area in the precordillera between Mendoza and San Juan. It has sometimes been thought to be Triassic in age, but is believed by Dr. H. J. Harrington (1941, 1956) to be Permian. A few fishes (Bordas, 1944) and a single footprint (Rusconi, 1951a, 1956, and Peabody, 1955) had been described from the Santa Clara, but no tetrapod fossils. We first camped near the puesto of Santa Clara, near the north end of the area covered by the formation, at the east margin of the precordillera in southern San Juan Province, and explored this area. Here the Santa Clara shales and sandstones, some thousands of feet thick, form a series of mountains separated by deep valleys. We found further remains of fishes in the area of original discovery, and a further fish locality in shales north of the Quebrada de la Montaña a short distance east of the boundary between the Santa Clara beds and the Villavicencio group. In addition, a series of trackways of rather poor quality was found and cast; these were situated a short distance up a senda leading south from the Quebrada de la Montaña to Puesto Alojamiento. But as far as our sampling of these vast exposures went, they appeared to be entirely barren of tetrapod osseous remains.

A second camp was made in the southern area of the Santa Clara Formation, in the canyon of the Río de las Peñas, between

Cerro Peña and Cerro Palado de las Higueras. Footprints had been previously reported from this area. We learned later that Sr. Bonaparte had made a visit to this area previous to ours. Like him, we found the region to be exceedingly rich in reptilian trackways, in a fashion comparable to areas of the famous Connecticut Valley Triassic. The trackways, however, are in the main obviously those of dinosaurs or advanced thecodonts, and the beds are presumably middle or late Triassic in age, despite the presence of "*Chirotherium*"-like footprints. As in the northern part of the Santa Clara Formation, we failed to find any bones; not even fish specimens were discoverable.

Bodenbender (1911, etc.) had described at length as "Paganzo II" a very thick series of red sandstones, presumably Permian in age, from La Rioja Province. These are present in the region of the Sierra de Sañogasta, its southern continuation, the Sierra de Vilgo, and the country south of the mountains, between the village of Paganzo and the railway junction of Patquia to the east. We spent many weary days walking these sandstones from the region of Patquia northward towards Chilecito, and in the region of Los Colorados railway station. We found not the slightest trace of animal life in these abundant exposures of "Paganzo II"; not a bone, not even a fish scale or a footprint. Following this discouraging period, we took time out for a brief visit to Tucumán, where we were hospitably received at the Instituto Lillo by Director Willink, and profited by discussion with Sr. Bonaparte.

Permo-Triassic beds had been studied in the Sierra de las Quijadas in northwestern San Luis Province by Sr. José Román Guinazú of San Luis, and footprints from this region were described by Lull (1942). The group spent some time there. The best exposures lay in a deep amphitheatre, difficult of access, west of Puesto Hualtarán. From the nearest approach by car there was necessary a long, tortuous walk, followed by a horse-trail descent of several hundred meters into the base of the amphitheatre; the return at the end of a day involved the wearisome ascent of the canyon walls. Here, as in other areas previously explored, not a bone was found, although a number of footprints of middle to late Triassic type were seen in the deepest and lowest beds of the area.

Permian sediments had been reported in the Sierra de los Llanos of southern La Rioja (Bracaccini, 1946). Here we found massive red conglomerates and grey plant-bearing shales. Neither type of sediment appeared promising as a possible source of

tetrapod remains, and only a very short time was spent in this area.

Having thus prospected for the better part of two months in some five areas with completely negative results, we had become somewhat disheartened. As some slight alleviation, we decided to visit for a short time our old "stamping ground" of Ischigualasto, for the purpose of collecting fresh material of rhynchosauroids, which by agreement with Sr. Bonaparte, I am studying. We had, in our discouragement, half come to believe that perhaps we had lost the ability to see fossil bones even if present. Ischigualasto disabused us of that apprehension; a good selection of rhynchosaur specimens was obtained.

The Christmas season had now arrived, and we stopped work to spend a few days at Samay Huasi. But despite the beauty and amenities of that place, the holidays were far from joyful for us. Half of our field time had been consumed, and we had thus far met only with utter failure.

But a complete reversal of fortune now occurred. Among the places remaining for possible investigation, one which appeared particularly attractive was an area in western La Rioja Province, west and south of Chilecito, west of the Sierra de Sañogasta, and about three hours distant from Chilecito by car. Here, at the east margin of the barren Campo de Talampaya, along the rivers Talampaya, Chañares, and Gualo, geological reconnaissance by Bodenbender (1911, etc.) and, in recent years, by de la Mota and Fidalgo (unpublished) had shown the presence of a varied series of sediments of Permian and Triassic age. No fossils had been seen, but in view of the considerable range in time occupied, and the probability of a variety of sediments in the succession of formations which appeared to be present, one might not unreasonably hope that vertebrates might somewhere be found.

This hope was abundantly justified. We first pitched camp in the southern part of the area, near the elevation known as the Mogote del Gualo and near the only spring of any importance in this arid region. On our first day of prospecting, fragmentary vertebrate remains were discovered; the next day several good specimens of dicynodonts came to light; from that day on until we stopped work some seven weeks later, not a day passed without the discovery of worthwhile reptilian material. From our first camp we presently moved some miles to the northwest to camp near the point where the Río Gualo emerges from the hills into the flat Campo de Talampaya. Finding that still richer fossil deposits were present farther to the north, in the valley of the Río

Chañares, we camped for the remainder of our stay on the banks of that stream.

In the following article in this series there will be given a resumé of the geology of the area. The region is only a short distance from the Ischigualasto Valley on the opposite, western, side of the Campo de Talampaya, and several of the later Triassic formations in the Chañares-Gualo region could be readily identified with the Los Colorados, Ischigualasto, and Los Rastros formations with which we had become familiar on our earlier trip. No fossils were found by us in the limited exposures of the first two; in the carbon-bearing Los Rastros a small amount of fish material was seen, and more could probably have been collected had we not found other, more profitable work. In rather lower beds, perhaps of Permian age, which we are terming the Tarjados Formation, fragmentary reptile remains were found in two areas, and not improbably intensive work would result in further finds. Nearly all our finds, however, were derived from a series of volcanic tuffs underlying the Los Rastros beds, which we are terming the Chañares Formation. These include some 75 meters of distinctive blue-white beds, easily traceable across the region despite the presence of numerous faults. Almost all the fossil remains, we presently discovered, occurred in the lowest 10 meters or so of these beds, and in most areas a careful following of the base of the Chañares resulted in the discovery of fossil specimens at frequent intervals. Some of the specimens were found simply buried in the tuffs. In a large proportion of cases, however, they were enclosed in grey-brown colored nodules of coarser tuffs. A fraction of such nodules proved to be barren; in some areas, however, almost every nodule would contain a skull or skeleton, and in some cases, two or three individuals would be represented in a single nodule. Never had any of us encountered a fossil-collecting area of equal richness. To add to our pleasure, it was obvious in the field that preparation of the specimens (unlike much of the material collected at Ischigualasto on our earlier expedition) could be readily accomplished.

Apart from a large dicynodont, almost all the specimens were forms of small size; the skulls averaged but a few inches in length. More than 150 good skulls were collected and, in addition, large amounts of postcranial materials. At the time this is written, little of the material has been prepared, but apart from

a relatively small fraction of "problematica," the general systematic position of most of the specimens was evident when collected. There appears to be but a single type of dicynodont, apparently of the general *Kannemeyeria* type. A considerable fraction of the finds were those of small thecodonts, some, at least, appearing to be forms on the pattern of *Euparkeria* of the *Cynognathus* zone of South Africa (recently redescribed by Ewer, 1965). The greater part of the collection, however, consists of small cynodonts; part of them are carnivorous, but the greater number are "gomphodonts," in which the cheek teeth form a grinding battery.

THE TRIASSIC FAUNAL SEQUENCE

The position of the Chañares fauna in the Triassic sequence will, I trust, become apparent as its components are described in future numbers of this series. Meantime, a brief discussion of our current knowledge of the sequence of Triassic continental vertebrate faunas seems merited. The Triassic is commonly divided into Lower, Middle, and Upper portions stratigraphically — or in chronologic terms, early, middle, and late — in agreement with the three-fold division of the European Triassic (as indicated by the period name) into Bunter, Muschelkalk, and Keuper. On the basis of marine faunas, a series of stages — Scythian, Anisian, Ladinian, Carnian, Norian, and (as a transition to the Jurassic) Rhaetic — have been erected. It is frequently attempted to fit the vertebrate faunas into this sequence of stages. For the most part, however, this cannot be done with any degree of accuracy, because of the rarity of actual continuity of beds containing continental vertebrate faunas with marine strata which can be assigned a definite place in the stage sequence; most of the stage names are derived from Alpine beds far removed from continental areas. The only major exceptions have to do with the "Eotriassic" Scythian zone. As both Watson (1942) and Lehman and others (1959) have shown, the *Cynognathus* and *Lystrosaurus* zones of South Africa are definitely to be regarded as "Eotriassic" and Scythian in age¹ mainly on the basis of labyrinthodonts; the Moenkopi of the early North American Triassic and the Bunter of Europe are equally well assignable to the

¹ Huene (1956) has at times tabulated the *Cynognathus* zone as middle Triassic, but has cited no reason for this.

Seythian on the basis of their content of labyrinthodonts — labyrinthodonts of types not too far removed from those of the "Eotriassic" of Greenland and Madagascar. At present it is perhaps best to avoid commitment of specific faunas to specific marine stages in attempting to define a continental vertebrate sequence.

In the early years of this century our knowledge of a Triassic vertebrate sequence was very limited. For the early Triassic, we knew little of continental forms (apart from amphibians) except in the Upper Beaufort (*Lystrosaurus* and *Cynognathus* zones) of South Africa. Here, therapsids, most notably a variety of cynodonts, constituted the bulk of the fauna; archosaurs, in the form of primitive or aberrant thecodonts, were present in modest numbers; other reptiles were small in numbers and variety. At the other end of the Triassic sequence, a late reptilian assemblage of very different nature, consisting almost entirely of dinosaurs and advanced thecodonts, was known from a variety of redbeds formations, such as the Keuper of Europe, the Newark, Chinle, etc. of North America, and the redbeds of the Upper Stormberg of South Africa. Between, continental faunas of possible middle Triassic age were practically unknown, for the European Muschelkalk is marine, other middle Triassic beds of the northern continents are also marine, and the Molteno of South Africa had yielded no fossils except plants.

With the predominance of therapsids in the early Triassic, and of thecodonts and dinosaurs toward the end of the period, it was generally assumed that middle Triassic reptile faunas, if and when discovered, would exhibit a simple transition between these two extremes, with therapsids on the wane and with thecodonts advancing and showing the beginning of the dinosaur radiation. We are now in process, however, of gaining from Africa and South America a seemingly representative series of middle Triassic faunas — from the Santa María beds of Brasil, the Manda beds of East Africa and, most recently, the Ischigualasto beds of Argentina. To some degree these faunas show expected intermediate characters, for they contain advanced thecodonts and the beginnings of the dinosaurs. But the faunas show striking positive characters. Therapsids are rather restricted in variety, but show a surprising abundance of "gomphodont" cynodonts. Equally surprising and striking in these faunas is the overwhelming abundance of rhynchosaurs, almost unknown in earlier or later beds.

While it is premature, I think, to tie them down to specific marine stages, or to characterize them as "early," "middle" or "late" in any restrictive way, I believe it is clear that there are three successive stages in the faunal history of continental Triassic vertebrates:

(A) An early assemblage, of which the faunas of the *Lystrosaurus* and *Cynognathus* zones of South Africa, and the Wuh-siang beds of Shansi (China) are typical. There are abundant therapsids, principally cynodonts — mainly carnivorous, but with a few "gomphodonts" with molar-like cheek teeth. Thecodonts include generalized primitive forms such as *Euparkeria* and aberrant archaic types such as *Erythrosuchus* and *Chasmosaurus*. Primitive rhynchosaurs are present but rare.

(B) The type of assemblage found in the Maleri, Santa María, and Ischigualasto beds. Carnivorous cynodonts persist, but are greatly overshadowed by abundant gomphodonts. Typical rhynchosaurs constitute a large fraction of the fauna. Thecodonts of advanced type are present, and a few early dinosaurs.

(C) The typical assemblages of the late Triassic, such as the Upper Keuper, South African redbeds, Lufeng series of Yunnan, Newark, Chinle, and Dockum of North America, and Los Colorados of Argentina. Therapsids are close to extinction. There are various advanced thecodonts, such as aetosaurids and (in the northern continents) phytosaurs, and numerous and varied dinosaurs, but rhynchosaurs are generally extinct.

One would, of course, expect assemblages transitional between these stages. It is probable, for example, that the Chañares fauna will prove to be intermediate between (A) and (B), and the same may be true of the Ntawere fauna of Zambia (Brink, 1963; Kitching, 1963). Of the faunas which we have listed under (B), that of Ischigualasto is perhaps relatively late, since several forms have already crossed the thecodont-saurischian boundary.

The typical (C) faunas are characterized in general by an abundance and variety of dinosaurs, the presence, in the Northern Hemisphere, of metoposaurs and phytosaurs, and the absence of rhynchosaurs and practical absence of therapsids. Certain beds usually placed in this category appear, however, either to be of earlier age than that of the typical (C) faunas, or else indicate regional late survival of certain of the forms characteristic of the (B) faunas. For example, the Maleri beds of India (Jain, Robinson, and Chowdhury, 1964) are generally assumed to be of relatively late Triassic age because of the presence of metoposaurs and phytosaurs. However, there is, in the restricted fauna

known, only one possible dinosaur, and rhynchosaurs persist. We may have here a (B)-(C) intermediate.

Baird and Take (1959) have recently discovered a reptilian fauna in the Wolfville sandstone of Nova Scotia, generally regarded as a basal member of the Upper Triassic Newark group. But quite in contrast with typical Newark faunas, Dr. Baird informs me that not only rhynchosaur remains, but a gomphodont, as well, are present. Quite surely we are here dealing with a fauna transitional between (B) and (C).

Rhynchosaurs are present in the Triassic fauna of the region of Elgin, Scotland, currently being restudied by Walker. Because of the close resemblance between *Stagonolepis* of Elgin and *Actosaurus* of the German Keuper, Walker (1961) believes the Elgin fauna to be late Triassic in age. There is, however, no reason to believe that the aetosaurid type of thecodont was particularly short-lived; it was already present in the Ischigualasto fauna (Casamiquela, 1960). Possibly the Elgin fauna is transitional between (B) and (C); but the absence of dinosaur remains, except for *Ornithosuchus* (Walker, 1964) — a form so primitive that it has generally been regarded as a thecodont — strongly raises the question as to whether the Elgin fauna may not really belong in the (B) category and be of middle Triassic age. Rhynchosaurs are known from several English localities which are classified as "Keuper." But it will be noted that there is no English equivalent of the Muschelkalk of the continent; the early Triassic "Bunter" equivalents are immediately followed by redbeds of "Keuper" type, and it is quite possible that part or all of the English rhynchosaurs are of middle Triassic age.

In sum, it appears to be a reasonable working hypothesis that the Triassic included a sequence of three successive continental vertebrate faunas characterized by a dominance of (A) therapsids, (B) gomphodonts and rhynchosaurs, and (C) dinosaurs. We cannot, of course, expect completely clean-cut distinctions between the three; but a clear pattern seems to be emerging.

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